

**NEUROBEHAVIORAL PATTERNS DURING ACTION
OBSERVATION AND EXECUTION OF COMPLEX
GOAL-DIRECTED MOVEMENTS**

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**NEUROBEHAVIORAL PATTERNS DURING ACTION
OBSERVATION AND EXECUTION OF COMPLEX
GOAL-DIRECTED MOVEMENTS**

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To the students and faculty of the Georgia Institute of Technology

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SUMMARY

The production and mastery of complex action begins with action understanding, a process which arises from the observation of others. The mechanisms through which humans engage in action understanding are still debated, and several conceptual theories, such as the direct matching hypothesis and teleological stance theory, attempt to explain the underlying mechanisms. Tool-use utilizes the visual streams and the frontoparietal networks in order to encode the visual features of the task and the control of grasp. Areas in the frontoparietal network have been associated with action understanding due to the presence of mirror neurons. The visual streams, a network that interconnects occipital, parietal, and temporal areas, encode object shape, size, orientation, and use as well as eye movements during the online control of movement. Prior to the execution of movement such as in tool use, one must engage in motor planning, a three stage process that consists of: 1) task recognition 2) coordination of required motor sequences, and 3) performance of the task. Second order motor planning requires both knowledge and planning of immediate task demands (first order motor planning) along with the planning of the subsequent steps during reach and grasp. The purpose of this study is to analyze the neurobehavioral encoding of action intent during action observation and execution of a second order motor task using electroencephalography (EEG) and eye tracking. The results may help us uncover the neurobehavioral mechanisms in action understanding that we can leverage and target for more effective neurorehabilitative therapies.

CHAPTER 1

INTRODUCTION

The process by which neural networks are activated in order to coordinate one's muscles and limbs to achieve the desired goal of a motor task is referred to as motor control. Prior to the execution of movement, one must engage in motor planning, a three stage process that consists of: 1) recognition of the task at hand, 2) coordination and planning of the motor sequence required to achieve the task, and 3) performance of the task.¹ Motor planning encompasses a concept referred to as praxis, the ability to perform a complex motor task depending on the goal and context in which one is situated. In order to carry out complex tasks with tools and objects, one must have a clear mental plan of the movements required to achieve the desired goal, which is referred to as action understanding.² There are several neural regions implicated in action understanding in humans, but the most prevailing system is the mirror neuron system (MNS). These neurons fire during the observation and execution of action and are localized in the ventral premotor cortex (vPMC) and inferior parietal lobule (IPL). Existence of this network is said to be an evolutionary adaptation that arose in order to mediate action understanding.²

Evidence of action understanding is shown in studies evaluating gaze behavior during the observation of movement due to the presence of predictive and anticipatory gaze patterns. A study by Elsner et al. which required participants to passively observe a series of reaching-grasping actions determined that while observing others' actions, our eye movements tend to be predictive of the action goals.³ This conclusion helped draw support for the direct matching hypothesis which suggests that observed actions are encoded into motor representations of that action within our own neural networks. In the realm of motor

planning and visuomotor coordination, gaze data revealed anticipatory saccades/fixation to the region where the participant would eventually place his/her index finger.⁴ These results support the idea that the gaze is a crucial component in motor planning and determining hand-object interactions.

Neuroimaging is an extremely valuable tool for studying the neural networks through which action observation and execution occur. Action observation has been suggested to generate internal representations of that action within an observer's motor system and utilizes the parietal-premotor system to encode these mappings.⁵ An earlier study by Kelly et al. sought to examine these neural patterns through the use of EEG on right and left handed people as they viewed a series of motor tasks in the first and third person perspective.⁵ Results from this study indicated that in right handed people, motor representations are encoded unilaterally whereas in left handed people, they are encoded bilaterally. This information is significant because it suggests that "cortical networks involved in understanding action outcomes are dependent on hand dominance."

The majority of research in the field of motor planning has centered around testing action understanding using simple reach and grasp tasks. Due to the highly dynamic nature of our environment, we use much more complex motor tasks to navigate our daily lives, and we must constantly adapt to and interact with these changes. Second order motor planning is of particular interest, as this requires both knowledge and planning of immediate task demands along with the planning of the subsequent steps during reach and grasp. Very few studies have examined motor planning of complex tasks that require second order motor planning. The purpose of this study is to analyze how action observation modulates the neurobehavioral encoding of context and grasp intent during action observation and execution of a second order motor task. More specifically, we would like to learn how action observation affects the visual encoding of a task during the

performance of a complex motor action and what types of neural patterns exist that may exert a directed control over gaze behavior and action understanding overall. Thus, we developed three main hypotheses: 1) Gaze patterns will be spatially organized in a manner that is predictive of the goal of the movement; 2) ESC grasp trials will elicit greater neural activity in both conditions compared to normal grasp trials; 3) Greater neural activity in frontoparietal networks will be elicited in action observation compared to action execution.

CHAPTER 2

LITERATURE REVIEW

Motor planning and action understanding are crucial to the proper execution of motor movements. During action observation and the execution of goal directed movements, neurobehavioral patterns provide a clear insight into the neural networks through which motor planning and action understanding occur. More specifically, the recording of gaze behavior through eye tracking in combination with recording of electrical activity in the brain through electroencephalogram (EEG) has been shown to be quite useful in understanding the underlying neural activity that occurs during motor movements. Tool use is an insightful way to study the genesis of problem solving, as it requires a two-step solution: first planning for future actions followed by using the tool to achieve a goal after it has been picked up.⁶ These two steps resonate with the principles of motor planning and action understanding mentioned previously. Previous studies have mostly focused on studying first order motor planning, which refers to changing the way in which one interacts with an object based only on immediate task demands. However, we hope to focus on investigating more complex tasks that require second order motor planning (planning for immediate and future task demands) and are more prevalent in activities of daily living.

The key to praxis, defined as the performance of an appropriate motor action in response to an environmental cue, is action understanding, which has been shown to rely on two main visual streams in the brain: the dorsal and ventral streams.⁷ The dorsal stream is responsible for the online, or feedback supplemented, control of movement as well as action recognition, while the ventral stream is responsible for object recognition.⁷ Because these streams have been found to be essential to the praxis network, this suggests that in

those with neurodegenerative diseases, these networks are impaired and/or damaged, leading to the inability to properly perform motor actions.

Unlike first-order motor planning, second order motor planning is the ability to identify and plan for immediate task demands while also incorporating subsequent task demands into the motor plan. An example of second order motor planning is a concept known as “end state comfort”, in which one adopts an initial uncomfortable posture to end in a final comfortable posture.⁸ For example, to hold a cup, one would adopt a thumbs-up grip to pick up the cup. However, if the cup were initially placed upside down, one would adopt an initially awkward thumbs-down grip to turn the cup right side up and in so doing, end with a comfortable thumbs-up posture. This concept is important for our research because action execution relies upon proper motor planning, and so, if one is unable to appropriately identify the need for end state comfort based on the environmental cues, there must be a neurophysiological basis behind why this “understanding” is not present.

Previous studies have analyzed gaze behavior as a means for identifying the neural basis behind how we observe and execute actions. One study sought to investigate how gaze behavior was affected by varying the speed and direction of a computer-generated block’s movement.⁹ This study found that during the tracking of an object, gaze has a predictive nature, always leading in front of the movement of the block. Drawing on this, we suggest that during object tracking, gaze is predictive of the eventual position of a motion, which is an essential characteristic of the oculomotor system. Another study tested the ability of young children and adults to track a visual target on a screen that was intermittently blanked.¹⁰ Researchers found that older subjects were more accurate at predicting the reappearance point of the target compared to younger subjects and posited

that this behavior develops due to the maturation of the cerebellum over time. In the context of our research, however, these results reaffirm previous studies that support the predictive nature of gaze during object motion.

Furthermore, the predictive nature of gaze also extends to goal-directed eye movements, a concept that suggests our eye movements are anticipatory of the goal of a hand-oriented action well before the hand reaches the goal. A study performed on great apes familiarized the apes to images of a human hand reaching towards one of two target objects versus a claw reaching towards the other target object.¹¹ Results of this study found that when the target object grasped by the hand was swapped with the position of the other object, great apes still made anticipatory eye movements towards the original target, regardless of position. The eye movements were proactive and goal-directed because of the idea that action familiarity enhances action understanding. Because the apes were more familiar with a hand, similar in appearance to their own, grasping objects, they were better able to comprehend the goal of the action and were thus more accurate in predicting which object would be grasped. The direct matching hypothesis can also be used to explain the neurobehavioral patterns of the apes: because observed actions are mapped onto motor representations of that action, familiar actions (hand grasp) are encoded better than unfamiliar actions (claw grasp).¹¹

A previous study by Natraj et al. focused on calculating the probability that gaze would lie within three areas of interest when subjects viewed a tool-object scene.¹² One important result indicated that gaze is most heavily weighted towards the object in the environment, followed by oscillation between the object and the “manipulative end” of the tool paired with the object in the environment. The manipulative end of the tool was defined

as the end that directly interacts with the object, such as a hammer head hitting a nail. Another important result of this study showed that within the manipulative grasp condition, there was more spatiotemporally weighted gaze towards the manipulative end of the tool, potentially showing that there is visual encoding of grasp intent. This study then concluded that there is an effect called “object-oriented action priming”, in which our gaze is indicative of our efforts to determine the interaction between a certain tool and object by darting back and forth. Thus, this study reaffirmed the goal encoding nature of gaze.

Neuroimaging has also helped investigators understand the neural encoding of action observation and execution. A study performed by the Wheaton lab utilized EEG to examine the neural activity of participants as they viewed images of tool-object pairings situated within different grasp contexts.¹³ There were four conditions present: No Hand (only tool and object), Hand (tool, object and hand resting in scene), Functional grasp (grasping the handle), and Manipulative grasp (grasping operant end of tool). Results indicated that when participants viewed images of tool-object pairings in the awkward Manipulative context, there was significantly higher left parietofrontal activity compared to the No Hand context. From this, a conclusion was drawn that there are two networks at play: a left parietofrontal motor network to process familiar tool-object associations and a right parietofrontal network to decode and process the unfamiliar Manipulative posture. Thus, this study helped support the idea that there are multiple streams in the brain used to process and understand action observation and execution.

Praxis is a very significant area of research as the Wheaton lab and collaborators strive to understand the means by which we plan and execute movement. While many people have the ability to recognize, plan, and execute required actions in response to

environmental cues, those with neurodegenerative diseases often lack this ability and thus are unable to navigate daily life as easily. Diseases such as Parkinson's, Alzheimer's, and stroke can give rise to apraxia, in which patients cannot successfully execute motor movements. We must first fully understand the networks that allow us to perform complex motor movements before we consider the most effective modes of rehabilitation for these individuals.

The studies mentioned above mainly focused on first order motor planning tasks that involved simple reach and grasp tests. However, in reality, many of the tasks we encounter in daily life require at the very least second order motor planning. Using gaze behavior as a window into cognition and motor planning paired with EEG to elucidate the different activation patterns associated with certain tasks, we hope to determine how action observation and execution are encoded and contribute to action understanding.

CHAPTER 3

METHODS AND MATERIALS

Subject Recruitment and Cognitive Testing

Healthy, right-handed subjects ($n = 7$) between the ages of 18 and 30 years old with no past medical history of neurological deficits or illnesses were recruited to participate in this study after formal consent was obtained per guidelines established by the Georgia Tech Institutional Review Board. After each subject was guided through the consent forms and informed of any potential risks, the subject was instructed to complete an Edinburgh Handedness Inventory in order to assess the degree of right handed dominance.¹⁴ Any subject without right hand dominance was excluded from the study since we are primarily focused on the encoding of unilateral motor representations. After the inventory was completed, each subject was instructed to perform a visuospatial mental rotation task in which they were asked to determine whether two 3-dimensional figures were either mirror images of each other or whether one figure was a rotated version of the figure adjacent to it.¹⁵ This task was presented in four levels of difficulty: easy (0° rotation), intermediate (50° rotation), intermediate 2 (100° rotation), and difficult (150° rotation) (Figure 1).

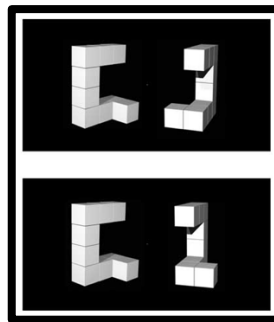


Figure 1. Mental rotation task. Top image shows two figures that are rotations of each other, while the bottom image shows two figures that are mirror images of each other.

After the mental rotation task, each subject was instructed to complete an online game called the Tower of London (Figure 2). The Tower of London task is widely used for the assessment of executive functioning, specifically planning. In this task, the subject must match a “target stack” by moving around a set of disks. Each subject was instructed to complete 26 trials of this game. An example of this game is shown below. Data recorded from this task includes the number of moves made to reach the target stack, the number of incorrect moves made, the number of moves required, and the duration to solve each problem.

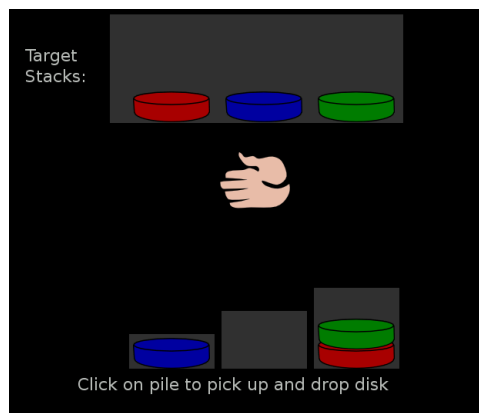


Figure 2. Tower of London task. The top portion shows the “target stack” that the subject must achieve. The bottom portion shows the set of disks that must be manipulated by the subjects to achieve the “target stack.”

The final cognitive test administered to subjects was the Test of Ability in Movement Imagery (TAMI), a test designed to assess subjects’ capacities for mentally picturing a series of movements.¹⁶ A series of movements was described, and each subject was instructed to choose the image that best matched the final position of the figure following the series of movements previously described (Figure 3).

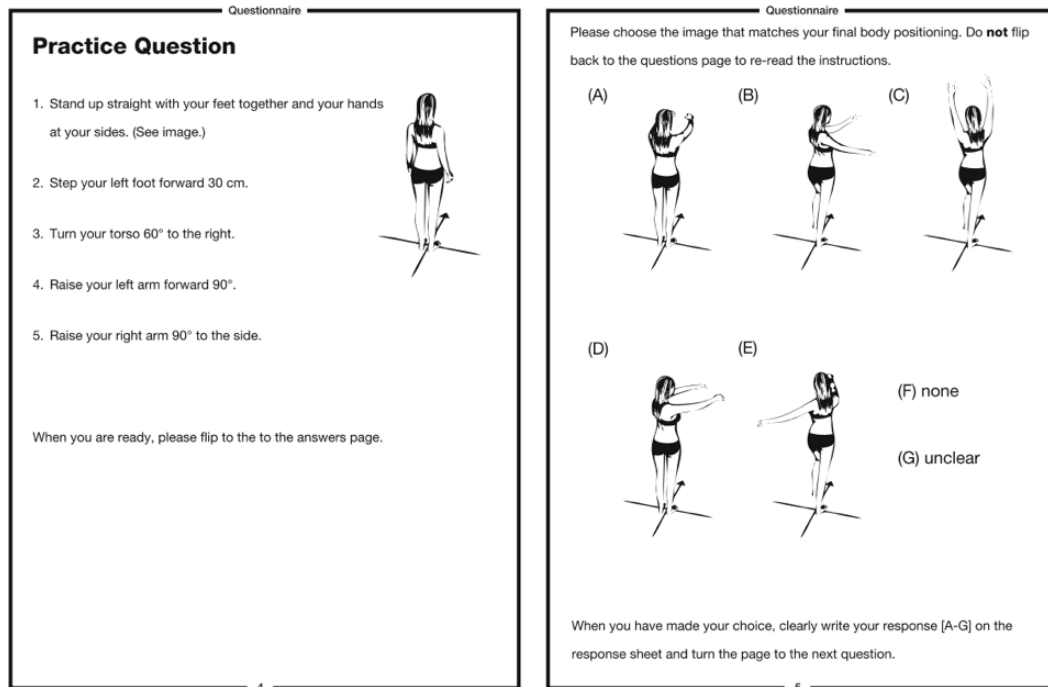


Figure 3. Example of TAMI test. Shown on the left, a series of body movements was orally described to the patient. Shown on the right, the subject must choose which image depicts the final position of the body after having executed the movements.

Subject Preparation

Electroencephalography (EEG) is a non-invasive method used to study the electrical activity of the brain. This neural imaging technique records small electrical potentials that arise from the brain using an array of electrodes place on the scalp. A 58-channel EEG cap was used to measure brain activity. Subjects were instructed to remove any earrings and/or hair ties. Alcohol wipes were used to clean both ear lobes, the forehead, and the areas inferior and lateral to the left eye. Ear and eye electrodes were filled with conductivity gel. Eye electrodes were placed on the lateral and inferior aspects of the left eye and secured in place with tape, while two ear electrodes were clipped to each earlobe. To determine where to place the most medial and anterior electrode, the subject's head was

measured from the nasion to the occipital condyle. Ten percent of the distance from the nasion to the inion was used as the location for the anterior electrode across all subjects to ensure consistent cap fitting. Sponge discs were placed on the front electrodes of the cap, and the cap was stretched over the subject's head, ensuring that the central electrode remained at the 10% nasion mark. A chin strap was attached to ensure the cap remains in place. The eye and ear electrodes were attached to the appropriate wires. Using a pumice scrub solution and long, wooden Q-tips, the subject's scalp was cleaned under all electrodes and to ensure hair was moved out of the way. Then, a syringe was used to apply electrode gel to all electrodes. All cables were then plugged into the head box, and impedance levels were ascertained using Neuroscan. If any electrodes were not within the desired range (less than 10 Hz), Q-tips were used to twist the gel within the electrode until the desired range was obtained. Subjects were then instructed to close their eyes, blink slowly three times, clench their jaw, move their eyes right and left, and close their eyes and multiply two large numbers. These actions were performed in order to detect changes in the EEG signals to ensure data was being recorded correctly and accurately.

To examine gaze patterns during task performance, subjects were fitted with Pupil Labs eye tracking glasses. These glasses have two small cameras pointed at each pupil, and a front facing camera recording a first-person world view of what the subject sees. The glasses were plugged into the recording computer, and the cameras were adjusted to ensure they were focused on the subject's pupils. The world view camera was adjusted to ensure that all parts of the work space were visible. To calibrate subject's gaze to the workspace, manual marker calibration ensured that the subject's gaze was aligned with any movements and all areas of the workspace. This process entailed instructing the subject to focus on a

small bullseye target in different locations spread out throughout the workspace until the glasses were calibrated at each point.

Experimental Paradigm

The experiment was conducted on a flexible workspace constructed by researchers in the lab. The workspace was set atop a table measuring 23.5 inches long, 39 inches wide, and 42 inches tall. Located on the top left and right of the workspace, two wooden boxes, called Base 1 and Base 2 were placed within the subject's reach. The top of each base contained openings in a particular geometric shape, such as a square or triangle. At the center of the workspace, a Rod with two shapes on either end was placed in between the two boxes (Figure 4). The subject was seated at the center of the table and positioned directly in front of a white Home Button (HB). In the center of the table and arranged below each base and the Rod, 3 circuit boards were fixed in place. These circuit boards were responsible for cuing the subject with LED lights and for recording removal and placement of the rod along the flexible workspace. The Home Button and the 3 circuit boards were connected to an Arduino, which controlled LED lights and recorded removal and placement of the rod. MATLAB and Arduino communication ensured that movement times and events were recorded and stored for future analysis.

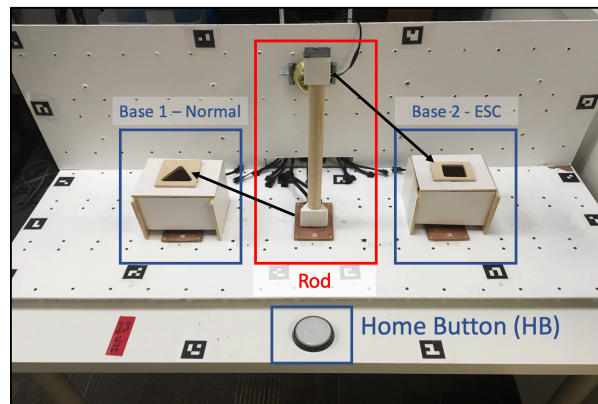


Figure 4. Flexible workspace setup for Task 1.

The timeline of each individual trial was structured as follows. A light would illuminate the Home Button, and the subject was instructed to press the button and keep it pressed. After 3.5 seconds, the “ready” signal appeared. This was indicated by each light at each base turning blue. Base 1 was located at the left most circuit board, and this was the normal grasp base. Base 2 was at the right most circuit board, and this was the end state comfort grasp base. Two seconds after the ready signal, the “set” signal would appear. This was indicated by either one of the lights at either base turning off, while the other light would stay on. The set signal indicated which base the trial would be focused towards. Two seconds after the “set” signal, the “go” signal would appear. This was indicated by the blue light turning either green (go) or red (no go). A green light would indicate that the subject should execute the task, while a red light would indicate that the subject should not perform the task and keep the home button pressed. If a green light was presented, the subject would take the Rod and place it into the base indicated by the signal and return to the Home Button and keep it pressed. A researcher would reset the Rod back on the center circuit board within 10 seconds of the subject placing the Rod in either base.

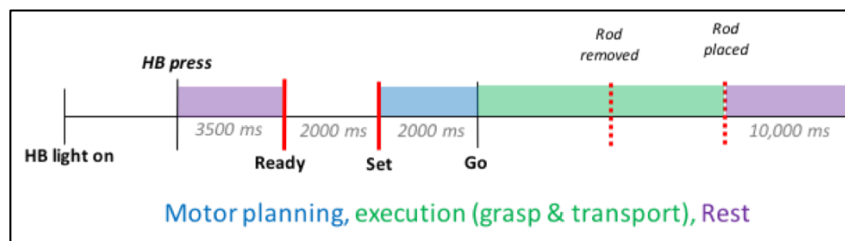


Figure 5. Single trial structure.

Subjects were randomly placed in one of two groups: action execution (AE) or action observation and action execution (AOAE). Subjects in the AOAE condition observed videos of actors performing the motor tasks that the subjects would later do themselves in between each block, whereas subjects in the AE did not watch any videos

and only performed the motor tasks instructed of them. Task 1 consisted of 3 blocks with 20 trials each, separated by 60 second breaks between the first and second block and the second and third block. Each block had an associated probability of having end state comfort trials, as shown in the figure below. Task 2 was structured in a similar way, however instead of using openings in the shape of a square and triangle, we used openings in the shape of a diamond for Base 1 and parallelogram for Base 2.

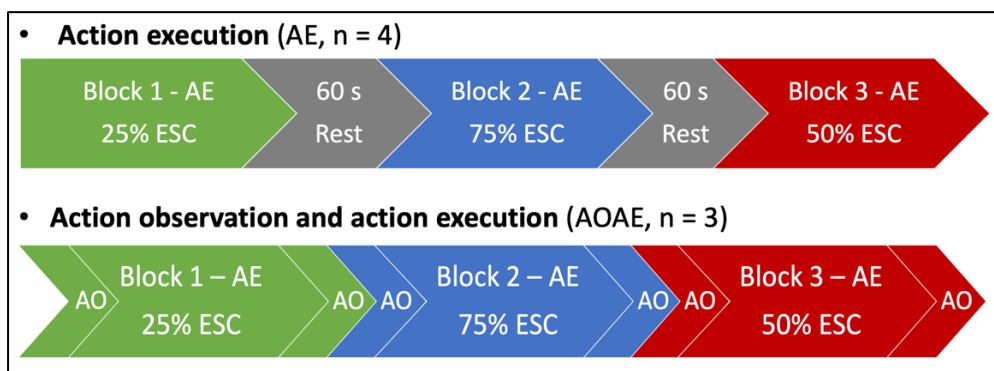


Figure 6. Experimental paradigm for AE vs AOA.

EEG and Eye Tracking Data Preprocessing

EEGLAB was used for the preprocessing of EEG data. This process consisted of filtering the data between 0 Hz and 30 Hz, assigning channel locations to the electrodes, re-referencing the data to the ear electrodes, and removing ground and eye electrode channels from the data. Artifact rejection was completed to filter out any background noise from the data and eye movements. The data was then epoched from 1 second before the ready signal for each trial to 8 seconds after the ready signal, which essentially means that the data was time locked to specific stimuli presented during the experiment in order to understand the neural responses associated with each stimulus. In the context of this experiment, our three stimuli were the ready signal, set signal, and go signal. Finally, the data was baseline corrected. Independent component analysis (ICA) was then performed

to decompose the data and examine the signal from each electrode for any sources of noise and conduct trial rejections. Event related potentials (ERPs), which are specific electrical signals generated in response to stimuli or events, were analyzed. In particular, we examined the P300 ERP component in the planning phase (time between set signal and go signal) due to its association with the evaluation of stimuli and “context-updating” of one’s model of the environment.¹⁷ Head maps depicting neural activity (μV) between 250 ms to 500 ms after the set signal was averaged across all trials for each subject. Based on the topographic activation map, the peak amplitudes (μV) of the P300 component were from electrodes in the left motor, left frontal, and left parietal areas.

Gaze data extracted from Pupil Player and MATLAB were used in conjunction to create areas of interest (AOIs) around both bases and the Rod. The amount of time that gaze fell within each AOI was then calculated for each individual trial, and this data was collected in a single spreadsheet for each subject and utilized for further analysis.

Statistical Analysis

Statistical analysis of eye tracking data involved the use of a linear mixed effects model in order to calculate main effects and interaction effects between AOI (Base 1, Base 2, Rod) and Condition (AE, AOAE). Tukey’s HSD test was used to calculate pairwise comparison. Statistical analysis of EEG data also involved the use of a linear mixed effects model in order to calculate main effects and interaction effects between Grasp (Normal, ESC) and Condition (AE, AOAE). Tukey’s HSD test was used to calculate pairwise comparisons. Significance was determined by a p-value less than 0.05, and a trend towards significance was determined by a p-value between 0.05 and 0.10.

CHAPTER 4

RESULTS

Gaze Behavior during Planning

In the Normal grasp trials, a main effect of AOI ($p < 0.001$), a main effect of Condition ($p = 0.367$), and an interaction effect of AOI and Condition was observed ($p < 0.001$). Pairwise comparisons revealed that gaze was directed significantly more towards the Rod than Base 1 in the AOAE condition ($t = -3.208$, $p = 0.014$). Furthermore, trends toward significance were observed as gaze was shown to be directed more towards the Rod than Base 1 in the AE condition ($t = -2.756$, $p = 0.053$) and more towards the Rod than Base 2 in the AE condition ($t = -2.586$, $p = 0.083$) (Figure 7).

In the ESC grasp trials, a main effect of AOI ($p < 0.001$), a main effect of Condition ($p = 0.3274$), and an interaction effect of AOI and Condition was observed ($p < 0.001$). Pairwise comparisons revealed that gaze was directed very significantly more towards the Rod than Base 1 in the AE condition ($t = -4.029$, $p < 0.001$). Gaze was also directed significantly more towards Base 2 than Base 1 in the AOAE condition ($t = -2.992$, $p = 0.029$), more towards the Rod than Base 1 in the AOAE condition ($t = -2.987$, $p = 0.029$), and more towards the Rod than Base 2 in the AE condition ($t = -2.962$, $p = 0.032$) (Figure 7).

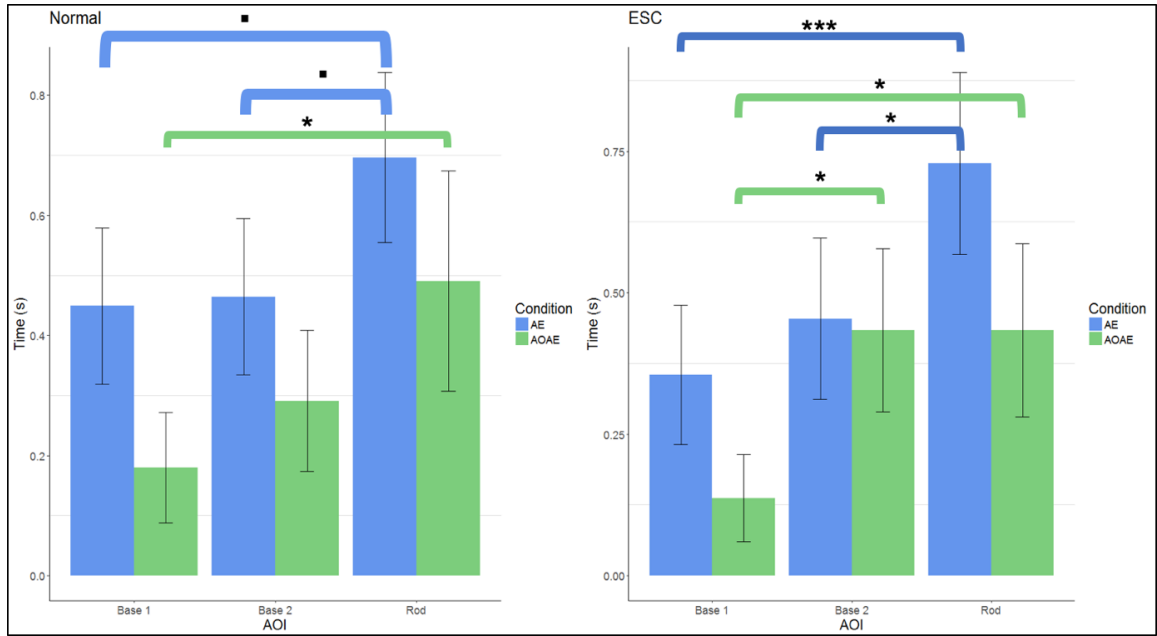


Figure 7. Spatial allocation of gaze. This depicts the amount of time gaze fell within each AOI, separated by grasp type. (***) indicates $p < 0.001$. (*) indicates $p < 0.05$. (.) indicates trends towards significance.

Topographic Distribution of the P300 Component during Planning

A topographic map of neural activation within the planning phase was generated to depict the mean activation of the P300 component from 250 ms to 500 ms after the onset of the set signal. A map was generated for Normal grasp and ESC grasp within each condition and averaged across all subjects within that condition. Figure 8 shows positive going potentials in the frontoparietal areas with more pronounced activation observed in AOA subjects. Based on these maps, we identified three regions of interest from which we analyzed peak amplitudes: left frontal, left motor, and left parietal.

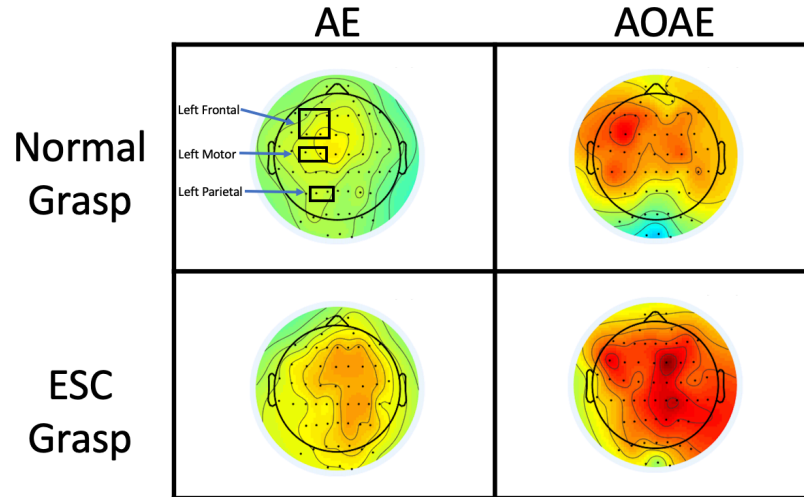


Figure 8. Topographic neural map of mean activation during planning.

P300 Peak Amplitude during Planning

In the left frontal region of interest, a main effect of Grasp ($p = 0.893$), a main effect of Condition ($p = 0.043$), and an interaction effect of Grasp and Condition was observed ($p = 0.0328$). The AOAE Normal grasp condition was found to exhibit greater peak amplitudes than the AE Normal grasp condition ($t = -2.665$, $p = 0.029$) (Figure 9).

In the left motor region of interest, a main effect of Condition ($p = 0.065$), a main effect of Grasp ($p = 0.212$), and an interaction effect of Grasp and Condition was observed ($p = 0.114$). The main effect of Condition demonstrates a trend toward significance with respect to the AOAE condition exhibiting greater peak amplitudes in both grasp types compared to the AE condition (Figure 9).

In the left parietal region of interest, a main effect of Condition ($p = 0.100$), a main effect of Grasp ($p = 0.111$), and an interaction effect of Grasp and Condition was observed ($p = 0.156$) (Figure 9).

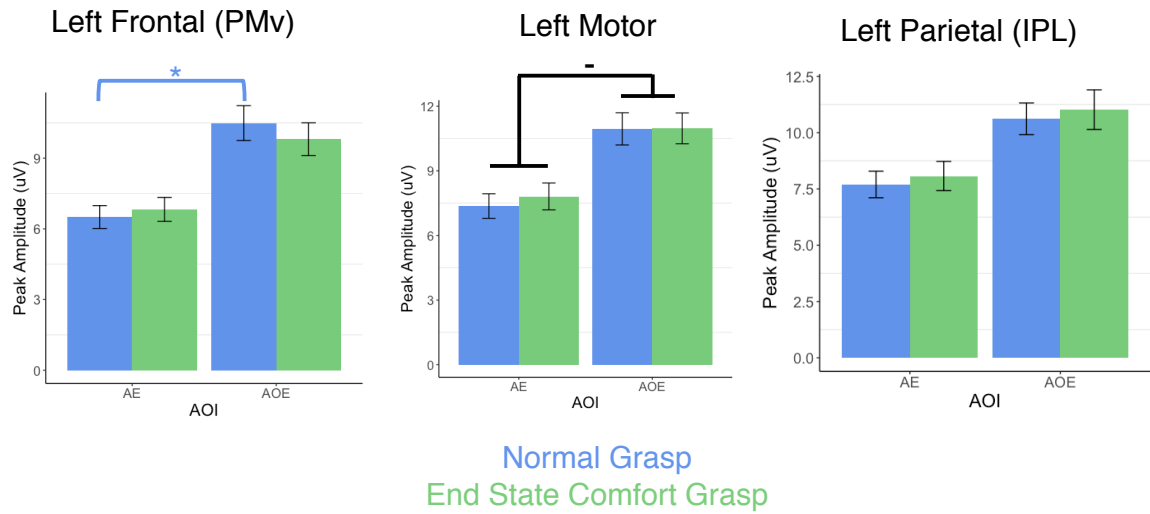


Figure 9. P300 peak amplitudes during planning phase. Peak amplitudes in each region of interest averaged across all subjects. (*) indicates $p < 0.05$. (-) indicates trend toward significance.

CHAPTER FIVE

DISCUSSION

The purpose of the current study was to evaluate how action observation prior to execution modulates the neurobehavioral encoding of a complex goal-directed task. Regarding the first hypothesis, preliminary analysis of eye tracking data revealed a spatial organization of gaze, however this hypothesis has not been accepted or rejected due to the need for further subject testing and analysis. Regarding the second hypothesis, results revealed no statistical significance in neural activity between Normal grasp and ESC grasp trials, and thus this hypothesis was rejected. Finally, regarding the third hypothesis, results did demonstrate greater neural activity within the AOAE condition compared to the AE condition in left frontal regions, and thus this hypothesis was supported.

Gaze Behavior

Regardless of grasp type, gaze results revealed that subjects in the AOAE condition directed gaze significantly more towards the Rod than Base 1. Subjects in the AE condition were also found to direct their gaze significantly more towards the Rod than compared to Base 1 or Base 2 while performing ESC grasp trials. This same finding is trending towards significance in Normal grasp trials for AE subjects as well.

Overall, these results indicate that subjects tend to be focusing their attention more on the Rod than any other feature of the environment while planning to perform the cued tasks. This suggests that task-relevant features (the shapes on either end of the Rod) and grasp-relevant features (Normal or ESC grasp) are taking priority as subjects perform the cued movements. Because the set signal immediately provides subjects with information about which base to move toward during each trial, they may be directing their gaze more towards the Rod in order to ensure they are adopting and encoding the appropriate grasp

type required of the task and that the correct end of the Rod is placed into the base. This seems to support our previous understanding that gaze behavior is anticipatory of a sequence of movements and that gaze is predictive of the goal of a movement.³ In the case of this experiment, during the planning phase, gaze is anticipatory of the hand reaching out to grasp the Rod with an appropriate grasp. While these results are still preliminary and limited due to sample size, further analysis may add statistical power to the results we have already found.

EEG

Results obtained from EEG recordings during the planning phase revealed that the AOAE condition demonstrated greater neural activity compared to the AE condition. More specifically, analysis of the left frontal region, which contains the ventral premotor cortex, revealed that subjects in the AOAE condition demonstrated significantly greater peak amplitudes while performing Normal grasp trials than subjects in the AE condition. This may reflect activity of the mirror neuron system as a consequence of action observation, since this collection of neurons is known to be housed in this area. Analysis of the left motor region revealed a trend towards significance with respect to AOAE demonstrating greater peak amplitudes in both grasp types compared to subjects in the AE condition. A previous study by Zhang et al. found that action observation can prime the motor cortex for execution in a similar manner as actual execution of a movement, and thus, the heightened activation in the AOAE condition within the left motor region may be explained by this priming effect.¹⁷ Analysis of the left parietal region revealed no statistical differences or trends in activation between the AE and AOAE conditions. Nonetheless, increased activity is seen with both grasp types within the AOAE condition compared to

the AE condition. A study by Johnson et al. reported that imagined grip selection of tools recruits a distinct parietofrontal circuit including mirror neuron structures, such as the IPL and PMv. Activation of this circuit may explain the stronger activation patterns seen in parietal areas within AOAE subjects.¹⁸

However, analysis of the EEG data through mean activation during the entirety of the planning phase, reveals that both the Normal and ESC grasp trials within the AOAE condition demonstrate greater overall activation (Figure 8). Interestingly, the head maps of the AOAE condition show bilateral activation whereas the activation patterns in the AE condition seem to be unilateral based on current data.

Overall, the findings of this study, while currently limited by sample size, provide support for the hypothesis that a bilateral frontoparietal attention network may be at play, modulating spatial attention while performing tasks. Previous research has demonstrated that the activation of a frontoparietal network may be involved with the updating of a “task-defined preparatory state” by modulating behavior upon cued tasks.¹⁹ For example, in the context of this study, the option to either adopt a normal grasp or ESC grasp may have been controlled by this network as the planning phase is characterized by the task to be undertaken. Concerning the P300 component specifically, previous literature has cited that the magnitude of the P300 increases with the amount of information able to be extracted from stimuli and the degree to which response preparation is required to perform a task. Thus, in our results, we may be observing greater modulation of the P300 due to competing grasp types as well as the various types of cues presented throughout each trial. Finally, an earlier study has also shown that EEG amplitude during the planning phase of a movement may be modulated as a function of the “number and spatial layout” of the potential

movements required to achieve a goal.²⁰ The heightened activity observed in left frontal, motor, and parietal regions may be a manifestation of the potential grasp types that may be adopted as well as the multiple bases in the environment that one must choose to move towards in order to complete the goal. In relation to action observation and understanding, the frontoparietal network of attention and mirror neuron system may be working in conjunction in order to create a clear internal representation of action.²¹

Future Studies

Currently, the results of this study are based on data collected from seven subjects. Further subject recruitment would significantly benefit this study as we may be able to add statistical power to any trends and patterns that we have already observed and perhaps identify more specific regions of interest to analyze. Additionally, analysis of ERP components besides the P300 may reveal novel neurophysiological processes behind motor planning and execution. The findings from this study may greatly benefit approaches to neurorehabilitative therapy for those who have developed ideomotor apraxia or other deficits related to motor planning as a result of stroke, neurodegenerative disease, etc.

REFERENCES

1. Liepmann (1900 and 1905): A Definition of Apraxia and a Model of Praxis, in: C.-W.W. Chris Code, Yves Joanette, André Roch Lecours (Ed.) *Classic Cases in Neuropsychology*, Psychology Press 1996, pp. 111-122.
2. R. Cook, G. Bird, C. Catmur, C. Press, C. Heyes, Mirror neurons: From origin to function, *Behavioral and Brain Sciences*, 37 (2014) 177-192.
3. C. Elsner, A. D'Ausilio, G. Gredebäck, T. Falck-Ytter, L. Fadiga, The motor cortex is causally related to predictive eye movements during action observation, *Neuropsychologia*, 51 (2013) 488-492.
4. A. Belardinelli, M.Y. Stepper, M.V. Butz, It's in the eyes: Planning precise manual actions before execution, *Journal of Vision*, 16 (2016) 18-18.
5. R. Kelly, J.C. Mizelle, L.A. Wheaton, Distinctive laterality of neural networks supporting action understanding in left- and right-handed individuals: An EEG coherence study, *Neuropsychologia*, 75 (2015) 20-29.
6. R. Keen, The Development of Problem Solving in Young Children: A Critical Cognitive Skill, *Annual Review of Psychology*, 62 (2011) 1-21.
7. L.J. Buxbaum, S. Kalénine, Action knowledge, visuomotor activation, and embodiment in the two action systems, *Annals of the New York Academy of Sciences*, 1191 (2010) 201-218.
8. K. Wunsch, M. Weigelt, A Three-Stage Model for the Acquisition of Anticipatory Planning Skills for Grip Selection during Object Manipulation in Young Children, *Frontiers in Psychology*, 7 (2016) 958.

9. M.C. Bulloch, S.L. Prime, J.J. Marotta, Anticipatory gaze strategies when grasping moving objects, *Experimental Brain Research*, 233 (2015) 3413-3423.
10. C. Ego, D. Yüksel, J.-J. Orban de Xivry, P. Lefèvre, Development of internal models and predictive abilities for visual tracking during childhood, *Journal of Neurophysiology*, 115 (2016) 301-309.
11. F. Kano, J. Call, Great Apes Generate Goal-Based Action Predictions, *Psychological Science*, 25 (2014) 1691-1698.
12. N. Natraj, Y.M. Pella, A.M. Borghi, L.A. Wheaton, The visual encoding of tool-object affordances, *Neuroscience*, 310 (2015) 512-527.
13. N. Natraj, V. Poole, J.C. Mizelle, A. Flumini, A.M. Borghi, L.A. Wheaton, Context and hand posture modulate the neural dynamics of tool-object perception, *Neuropsychologia*, 51 (2013) 506-519.
14. R.C. Oldfield, The assessment and analysis of handedness: The Edinburgh inventory, *Neuropsychologia*, 9 (1971) 97-113.
15. G. Ganis, R. Kievit, A New Set of Three-Dimensional Shapes for Investigating Mental Rotation Processes: Validation Data and Stimulus Set, 2015.
16. A. Singhal, Introducing TAMI: An Objective Test of Ability in Movement Imagery AU - Madan, Christopher R, *Journal of Motor Behavior*, 45 (2013) 153-166.
17. J.J.Q. Zhang, K.N.K. Fong, N. Welage, K.P.Y. Liu, The Activation of the Mirror Neuron System during Action Observation and Action Execution with Mirror Visual Feedback in Stroke: A Systematic Review, *Neural Plasticity*, 2018 (2018) 14.

18. S.H. Johnson, M. Rotte, S.T. Grafton, H. Hinrichs, M.S. Gazzaniga, H.J. Heinze, Selective Activation of a Parietofrontal Circuit during Implicitly Imagined Prehension, *NeuroImage*, 17 (2002) 1693-1704.
19. P. Praamstra, L. Boutsen, G.W. Humphreys, Frontoparietal Control of Spatial Attention and Motor Intention in Human EEG, *Journal of Neurophysiology*, 94 (2005) 764-774.
20. P. Praamstra, D. Kourtis, K. Nazarpour, Simultaneous preparation of multiple potential movements: opposing effects of spatial proximity mediated by premotor and parietal cortex, *Journal of neurophysiology*, 102 (2009) 2084-2095.
21. W.M. Land, D. Volchenkov, B.E. Bläsing, T. Schack, From action representation to action execution: exploring the links between cognitive and biomechanical levels of motor control, *Frontiers in computational neuroscience*, 7 (2013) 127-127.